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BACTERIOLOGY IN ITS GENERAL RELATIONS.[1]

BY H. L. RUSSELL.

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Quite naturally, the practical application of bacterial research has been primarily directed along the lines of medicine and the industrial activities. In any new branch of scientific progress, this is almost invariably the case. Our interest in the subject is largely measured by what it is worth to us, and in proportion as it fills this function do we estimate the importance of its study. The results that have already been accomplished in bacteriology have not however been entirely confined to the applied side of the subject. The cause of pure science has also been greatly advanced in various ways. The correlation of any branch of science with allied subjects is to-day so intimate that any discovery in one, often furnishes valuable suggestions in kindred lines of research. It is in this light that we may consider the effect that bacteriology has had upon the greater subject of biology, taken in the pure not the applied sense, and if possible point out some of the lines which seem to promise a rich fruitage from a general biological standpoint. It can hardly be expected that so young a member of the biological family could as yet have contributed much to the common fund that all its workers are striving to accumulate, yet it may with justice be said that the circle of its influence has widened much beyond its own particular sphere. Perhaps the most valuable of the contributions to its sister branches has been in its *technique*. This influence has been most strongly marked in the closely related departments of botany. The excessive minuteness of bacterial forms and the ubiquity with which these organisms are distributed made it absolutely necessary that some reliable means of pure cultures should be introduced before much real advance could be made in this subject. In bacteriology; this

[1]Delivered before the Biological Club of the University of Chicago, Feb'y, 1893.

found its greatest development in the employment by Koch, of gelatin as a transparent solid medium for the isolation and cultivation of germs. Some features of this method had been anticipated by other workers, especially Klebs.

This method enables the experimenter to isolate the form he desires to study from any mixture of different species, and by cultivating it in sterile media, a pure culture derived from a single germ can be obtained which is made the basis of definite morphological and physiological study. Brefeld's methods of studying the morphology and developmental history of the fungi are essentially the same as the bacteriological culture methods. He first obtained his pure cultures by dilution until he had a single germ. Later he added the use of gelatine or other transparent ingredients as a means of isolating and fixing the developing organism. The results of these studies which now fill ten large quarto volumes, are among the greatest contributions to mycology, that this century has produced. He refused to admit the validity of the classic descriptions that had been based upon material gathered under natural conditions, maintaining that the systematic part of the science was full of errors, that had arisen from the examination of imperfect mixed growths, and the separation of different growth-forms into individual species.

Basing his opinion upon the only scientific foundation, that we must know the *complete* life history of a form before we can intelligently study its phylogenetic affinities, he made his observations upon pure cultures grown from a single spore in sterile nutrient media. These he kept from the original spore until in many cases the fruiting process had been completed. By this method he was able to settle definitely many disputed points concerning the value of certain form-genera and species. These conclusions of Brefeld, based upon the single cell, pure culture method, have revolutionized the entire classification of the great group of fungi and the theories as to the phylogenetic affinities of different groups have been greatly modified. Hansen adopted the same method in his study of ferment organisms, more especially the yeasts, and this plan of pure culture growths has settled many controver-

sies in the biology of this imperfectly understood group. Beyerinck applied the gelatin method in the isolation of algæ and succeeded in cultivating a number of free unicellular forms, some symbiotic species in certain hydra and paramœcia, and a number of the gonidia in lichens. So far all attempts to apply the isolation methods of solid media to animal life have proven futile. Strenuous efforts have been made upon such parasitic forms as the malaria plasmodium and other parasitic protozoa, but as yet these experiments have not been successful.

With respect to tinctorial methods, bacteriology has been of service. The art of staining to bring out structural differences more clearly has been systematically developed in the latter half of the present century. The discovery of aniline colors in the seventies gave an additional impulse and the names of Koch, Ehrlich, and Weigert will always be associated with the rapid advance and development of this branch of biological technique. The necessity of staining in order to differentiate bacteria in animal tissue has been so imperative, that much time and effort have been expended in order to improve the old, and discover new processes. The success of these efforts has been stimulating in other lines of work, and has materially advanced the general knowledge of stains.

Koch in 1878, was one of the first to apply photography to the study of microscopic preparations. The application of this process by means of photograms for class demonstration, and the obvious advantages that it possesses for accurate illustration are apparent. The recently completed photomicrographic atlas of bacteria by Fränkel and Pfeiffer exemplifies the degree of excellence that has already been attained in this branch.

In the study of bacterial forms, the old types of microscopes were entirely inadequate. The necessity of improved instruments, in regard to definition and resolution to work out the structure of these "infinitely little" organisms, acted as a healthy stimulus on the art and science of lens making. The perfected instrument of to-day, with its homogeneous immersion, the Abbe condenser, and the apochromatic objective, are largely the result of the demand of bacteriologists. These

points suffice to show the influence that the study of the bacteria has exerted upon the technique of other lines of biological thought.

Has it been able to any extent to aid in the solution of any of the general questions that have from time to time engaged the attention of all students of living phenomena? In considering this, reference will be made mainly to those lines that are of special importance in the theoretical problems of biology. As has been previously stated, the main results of bacteriology as yet are found in applied science, but the germ theories of fermentation, of nitrification, of sewage filtration, of nitrogen fixation, of the etiology of contagious diseases and of inflammation are monumental witnesses of the value of this department in the realm of pure science.

Bacterial methods in the hands of the illustrious Pasteur were the means of combatting and effectually routing the heterogenists from their defence and proving beyond the shadow of a doubt, the accuracy and universality of the Harveian motto "*Omne vivum ex vivo.*"

Since the discovery of the laws, which are the foundational basis of the doctrine of evolution, every department of natural science has paid tribute to it, adding fact upon fact, and broadening the basis of the principles, formulated by the observant Darwin. Morphology and physiology in both branches of biology, as well as pathology, have furnished their quota of proof in this grand advance step in knowledge. Has bacteriology contributed its contingent to the general result on this and other vital problems? Does the testimony of the infinitely little corroborate that of the higher and more complex forms of life?

The advantages of this group as types for study on many questions of this nature, have not as yet been generally appreciated. The practical side of the subject has naturally presented the most attractive phase, and even the systematists have found but scant encouragement for their labors, except for the utilitarian purpose of species determination.

The number of observers who have made this group of organisms a subject of special study with reference to general biologi-

cal laws have been but few. Valuable data have however, often been obtained in an incidental way. The possibilities, which this group of organic life offers for the study of many of these general problems, are so noteworthy that it seems worth while to call attention to them more in detail. In selecting forms for the study of certain questions, the biologist chooses, as far as possible, the primitive generalized types upon which to base his observations. Specialization of form and function complicate the conditions and render it more difficult to apprehend the fundamental truth. In this respect bacteria occupy a unique position. Morphologically considered, they are a lowly organized and generalized type, while functionally, they possess a marked degree of specialization.

With our present appliances but little difference can be detected in form between many species that possess widely divergent physiological functions, so that species are often found that are morphologically similar and their dominant physiological function may be expressed either in pigment production, fermentative action, or in an infectious malady.

A certain degree of adaptability in an organism is also necessary if we are to subject it to prolonged experimentation. Many plants and animals are so susceptible to any modification in their surroundings that they cannot well be utilized for purposes of experimentation, a slight change often being sufficient to produce a cessation of the vital functions. Bacteria possess an adaptability not to be found in any other class of organisms. With a large proportion of these forms, the range in temperature of the limits of growth far exceeds any of the higher forms of life.

The majority of species are able to vegetate between 10° C. and 50° C. while exceptional ones grow at the freezing point and others thrive at a temperature of 70° C. This tenacity of life, far surpassing all other forms of animate nature, is as distinctive in the chemical as in the physical environment of these germs.

Another peculiar characteristic, that renders them of especial value from an experimental standpoint, is their rapidity of multiplication. A single cell is the progenitor of millions

in twenty-four hours. We can therefore accumulate the effect of certain external influences upon an almost infinite series of generations within a limited time. The time element, which in higher forms of life often necessitates the extension of experiments over a period of years owing to the relative slowness of reproduction, is here minimized to such an extent as to be brought entirely within the limitations of a single observer. By a rapid successive transference of cultures to fresh media, we can secure the effect of an experiment covering an immense number of generations within a limited space of time. Of course, the absence of sexuality in the reproductive process narrows the sphere of investigation, but there is no valid reason why as valuable results may not be obtained by experimental work on problems of variation and heredity as have been already accomplished with asexually propagated plants, like the sugar cane, banana, and potato. The objection that might be raised, that the morphological and physiological characters are more plastic, and therefore more easily modified than higher specialized forms of life, seems to be answered when we take into consideration the number of generations that intervene between the original type and the establishment of a pronounced variety. The gardener is able to modify the constitution of his plant by cultivating it under special conditions for a few years to such an extent that he produces a horticultural variety in a limited number of generations. The bacteriologist in his "microscopic horticulture" finds it far more difficult to modify his species to the same extent in a limited number of generations.

The ease with which experimental conditions can be modified in the manipulation of bacteria is also a valuable factor. The physical and chemical environment can be so rigidly controlled that the variability of conditions which is so disturbing a factor in experimental work on higher forms is practically excluded.

These are some of the evident advantages that bacteria possess for experimental research in evolutionary biology. It may be proper in this connection to state a few of the results which have been obtained in this field and which bear more

or less directly upon some of the more general questions of biological importance. As has been before intimated, so little direct attention has been given to this subject, that we are scarcely able to predict what results may be expected from the study of these problems from a bacteriological standpoint.

But few laws in nature have a wider expression than that of variation. In fact, it may be said to be co-extensive with life itself. Among the higher complex forms, no two individuals are exact counterparts of each other, but as one passes from the higher to the lower forms of life, the individual differences gradually become obliterated in the more generalized types, and a greater uniformity seems to prevail among the different members of the same species. In such simple protoplasmic elements as the bacteria, all individual variation is concealed, yet, it is presumably present, and were our facilities for recording such infinitesimal variations, sufficient, we would be able to detect structural and functional differences in each cell.

It is too early for us yet to say, whether the evidence that bacteriology may yield will be in favor of the "innate tendency of species to vary," or whether we are to regard variation as an "expression of the influence of environment." An almost untrodden field is before us which lends itself readily to experimental conditions and it is highly important that we interrogate Nature through the medium of investigation upon her more minute, as well as her larger forms of life.

Structural modification expressed either in change of external form or internal characters is usually made the basis for specific differences, so that classifications have been built more upon morphological, than upon physiological characters. A modification then of characters possessing a morphological value would be indicative of a profound change in the constitution of an organism. How far this would be appreciable in the case of bacteria is not definitely settled. A certain amount of form variation, (much more in some species than in others) is to be seen when different media are used for cultivation. Whether these manifestations are merely modifications due to

nutrition or not, it is difficult, if not impossible to say. The question may fairly arise, whether they are due to variations in the food medium or are they entitled to the dignity of varieties and species in the taxonomic sense.

Reproduction is considered one of the most complex and deep seated phenomena, of organic life. If we are able experimentally to change the inner constitution of an organic structure to such an extent as to permanently modify its reproductive function, we may justly conclude that a profound change in the original type has been induced. This has been done in the case of the anthrax fever germ. The bacillus that causes this malady is characterized by the ease with which endospores are produced. With a favorable temperature and free oxygen, spores are formed in the vegetating filaments in the course of from 24 to 36 hours. Roux succeeded in producing an asporogenous race of this bacillus by growing them in a nutrient culture medium to which potassium bichromate had been added in the proportion of 1 to 2000. He also succeeded in modifying this reproductive function by the use of phenol. Cultures containing 6 parts of phenol in 10,000 produced endospores in a normal manner, while those seeded in 20 parts to 10,000 were destroyed. Between these limits, the cultures maintained their vitality and grew, but in no case formed spores. When these asporogenous cultures were re-seeded into normal media, they vegetated in a normal manner but did not form spores, although the conditions were most favorable for the process. Behring succeeded in obtaining the same results by the use of rosolic acid. What these observers accomplished by the strict control of cultural conditions, Lehmann observed under more natural conditions. He found that certain cultures that had been cultivated in Koch's laboratory for many generations on gelatine exclusively had lost their ability to produce spores, but their virulence had not been impaired in the least degree. They could not be distinguished from the normal spore-bearing forms in any other than this particular. He tried to modify these varieties, and when the asporogenous type had been grown on a medium suitable for spore production, like potato, for a series of gener-

ations, he finally succeeded in producing forms that contained minute spherical refringent bodies, which in some cases externally resembled true endospores, but *biologically* differed from them materially as they were destroyed by heating for two hours at 60° C while the normal endospores are among the most resistent bodies known. This is a well authenticated instance, where the morphological character of reproduction has been modified, while the salient physiological features of the germ remained constant. This change had evidently been brought about through the influence of exterior conditions, and so deeply had the inner constitution of the germ been affected that it transmitted the character to its progeny although the normal conditions of development did not favor its production.

Were we to admit the evidence of physiological variation, we would find abundant proof among the bacteria that this group of organisms were more or less profoundly modified in their functional characters. Physiological variations have so far received but slight attention at the hands of biologists, but in bacteriology the truth of De Varigny's words that species must be defined not only by means of their anatomical characters, but also in terms of physiological differences, has been amply confirmed. Bacteriology has been forced to add physiological to the morphological diagnosis in the study of these minute forms.

That there is a variation in the characters of certain forms in a perfectly natural state is readily seen in the case of some contagious diseases like cholera. It is known that the peculiar individualities of the cultivations isolated from the different epidemics are so marked, that an expert can tell at a glance whether the culture in question descended from the germ found in the Naples outbreak, or in Egypt, or from India. As one epidemic is often the result of the transference of germs from another, and the two germs therefore more or less related, it is reasonable to infer that environment has much to do with their modification. But we are not confined to the evidence of physiological variation as afforded by examples under natural conditions. These conditions are too fluctuat-

ing and variable. It is only under rigid experimental control that we can obtain positive proof on this question.

The most noteworthy changes are those that show a decided modification of the physiological function of virulence. Nearly every species belonging to the pathogenic class is subject to greater or less variation in this respect. Anthrax fever, the classic example in bacteriology, has been shown by the experiments of Chauveau to vary in virulence to such an extent that from the original virulent culture, varieties or races have been grown that possess every shade of virulence from the deadliest type to that which is perfectly innocuous. These attenuated types maintain their newly acquired function in a perfectly constant manner, so that we have races of the germs that are christened " mouse anthrax," because they are pathogenic for mice only; others less attenuated are able to kill guinea pigs or rabbits, while still others are virulent for all classes of susceptible animals.

With many germs the variation of this functional property occurs quite readily in cultures under ordinary conditions, as in the case of pneumonia and hog cholera, where all degrees of virulence may be found. Sometimes abnormal conditions of environment seem to be necessary to produce the variation. These modified forms may persist only so long as the artificial conditions are maintained, reverting to the original type when restored to their normal environment, or in some species the constitutional characters of the germ are so changed that they are perpetuated although the conditions favorable to atavism are present. What is true concerning the variation of the pathogenic function is likewise true in regard to other physiological characteristics.

The chromogenic property of certain forms has usually been considered of diagnostic value, but in some instances spontaneous sports occur, as in *Bac. pyocyaneus* α and β, where the only observable difference is that the pigment produced in one is a bluish green, while in the other it is a fluorescent green, and quite distinct from the first. This species has been modified artificially so that the color producing power of the organism has been permanently abolished. From other chromo-

genic species like *Bac. prodigiosus*, the germ that causes "bleeding bread" and *Bac. cyanogenus*, that which provokes the disturbance known as "blue milk," varieties have been produced by constant selection and cultivation of cultures in which the color producing quality of the germs entirely disappeared. Laurent modified the chromogenic function of the Kiel water bacillus by exposing it to direct sunlight for a limited time. The suppression of this peculiarity was transmitted from generation to generation so that a perfect albinotic variety was formed. The color property was also lost when cultivated at blood heat and was not regained when continued cultivation was carried on at lower temperatures. These examples indicate the plasticity of this physiological function of color production and show the influence that is exerted upon the germ by a continued subjection to certain experimental conditions.

The objection may be raised that these cases that show a change in the various vital functions do so because their vitality is impaired and that the variety so produced is merely a degenerated and weakened type. While this may be true in certain cases, it does not detract from the value of such experiments as throwing more light upon the question of environmental influence. Besides, the rule is by no means general that loss and abatement of physiological function is correlated with degeneration. We have numerous instances among the pathogenic forms where greater luxuriance in growth is to be noted in connection with the mitigation of the powers of virulence as for instance in tuberculosis where cultivation on media containing glycerin-agar diminishes the virulence of the form while it increases the powers of growth. This can be explained as a case of partial reversion of the species, specialized in the direction of the pathogenic property to an ancestral saprophytic mode of existence.

The zymogenic, or fermentative function of bacteria has also been experimentally modified. The cultivation of the lactic acid bacillus, the germ causing the souring of milk, for a time in non-fermentable solutions, entirely destroys the property of decomposing the sugar in the milk and converting

it into lactic acid. When grown continuously on solid media it likewise loses the power to peptonize or liquefy gelatin, a character of such importance that it is used as a basis for classification.

This variation of function is very marked in the case of some of the marine bacteria.

One Mediterranean species, *Bac. halophilus*, grows only with the greatest difficulty on media that contains less than the normal percentage of salt in sea water, while on media made with sea water it thrives luxuriantly. Constant cultivation however on ordinary media finally so changed its habits that in the course of twenty generations, it flourished as vigorously when supplied with fresh as with salt water.

Another case has recently come under my notice that presents even a more marked change. *Cladothrix intricata*, a common form in the Mediterranean mud was first isolated some 18 months ago. It then manifested no particular preference as to the amount of salt necessary for development, growing equally well on fresh as on salt water media. Since its isolation, it has been kept in stock on agar made with distilled or tap water. This season when an attempt was made to transfer it again to sea water media, it failed to grow. At first, I thought the original stock culture dead, but examining it microscopically I found that all vegetative forms had died, leaving innumerable spores. Seeding an ordinary agar tube from this spore-bearing stock, within 24 hours a copious characteristic growth of the germ was obtained. A second attempt to transfer the germ from the fresh culture, containing only *vegetative* forms was equally unsuccessful. In this instance, not only had the organism lost the ability to germinate when supplied with salt water food but even the vegetating bacilli died when introduced into this medium. This might not be surprising in ordinary terrestrial or fresh water saprophytes, but in a form originally a marine species, it shows a marked modification of nutritive conditions.

Examples like the above indicate that physiological and morphological modifications are so closely related to the environment of the species that it seems almost impossible to

avoid the inference that there is some direct connection between them. Our ability to so rigidly govern the experimental conditions makes the case much stronger for these conclusions, than in those cases where the variations occur spontaneously. Whatever may be the true cause, or causes, that lead to variation among species, it cannot be denied that experiments from all classes of organic life will be valuable in adding to the store of observed facts, and thus giving us a broader basis upon which more accurate generalizations can be made. The evidence already at hand from the realm of the bacteria is promising enough to lead to the conviction that continued experimental work with reference to the problems of variation will be fruitful in results.

Few problems in biology are more prominent in the discussions of to-day than those pertaining to the subject of heredity. Among the different phases of this subject none hold a more important place than the doctrine of the transmission of acquired characters. The difficulties of the question are largely increased by our inability to define exactly what is meant by an acquired character. Under ordinary conditions, it is not easy to sharply differentiate between a variation brought about by an inherent tendency of the organism to vary, and one that is impressed upon the organism from without. We have however in the phenomena of artificial immunity, whereby a susceptible animal is rendered refractory toward a specific disease germ, a favorable field for the study of this problem. Artificial immunity is *par excellence* an acquired characteristic, as it is a deep seated and permanent change in the constitution of the animal that is produced through the influence of an exterior force. Several instances are on record that claim the transmission of acquired immunity in animals from the parent to the young. Chauveau found that the artificial immunity conferred upon goats was transmitted to their progeny but these cases are not pertinent to the problem of the transmission of an acquired character, for the possibility of a direct transference of the immunity by means of the body fluids is not excluded. All cases of the so-called transmission of artificial immunity that are conferred upon pregnant ani-

mals are open to the same objection. That the immunizing substance does permeate the entire body so that even the secretions are affected has been recently proven by the experiments of Ehrlich. He has recently shown that young mice may acquire immunity against that toxic alkaloid, ricin, by being nourished upon the milk of their mother, which has been artificially immunized. He obtained similar results with the tetanus bacillus, by immunizing a mother mouse with serum from a horse when the young were 17 days old. In 24 hours, one of the suckling young was infected with virulent tetanus spores from which it experienced no ill effect, while a control died in 26 hours. Two and three days after the mother had been immunized, other of the young were also tested, and it was found in these cases that the immunity was also transmitted from the mother to her progeny.

If the injection of the immunizing substance into the body of an animal can so permeate the tissues as to reappear in the secretions in 24 hours, it would seem highly probable that the immunity claimed to be transmitted by inheritance might be regarded as passing directly from the mother to her young rather than by means of the germ plasm.

The same objection applies to those cases where infectious diseases are claimed to have been transmitted. Wolff has recently subjected all of these cases to the closest examination, and he finds that only in a very limited number is there any probability that infection is ever transmitted from parent to progeny. In numerous cases of so-called inherited disease, he has actually determined lesions of the placenta, that allowed a direct passage of the germ. He claims that in no case has it been thoroughly proven that disease has been transmitted by the germ-plasm, although it is possible that either male or female generative cell may be diseased, and thus an infection, which he calls *conceptional* may take place.

Ehrlich has recently made some very interesting observations that have a direct bearing upon this question of acquired characters. They possess the advantage of approaching the subject in a fundamental manner, and while they are not numerous enough to justify general conclusions, they are of

great interest as indicating what may be expected from a further study of this subject.

In this case, he experimented with ricin and abrin, those toxic vegetable alkaloids that are so closely related to the poisonous products of bacterial growth. The question at issue in his experiment was, whether the male or the female cell, if either, possessed the ability to transmit artificial immunity to its progeny. His methods were, to first pair a highly immunized male rabbit with a normal susceptible female, and determine whether the progeny possessed any immunity against the toxic substance. In this series of experiments, he found that the descendants invariably succumbed when inoculated with the ordinary fatal dose. From this it is evident, he says, "that the idioplasm of the sperm is not in condition to transmit acquired immunity."[2] He then took up the more complex problem of the inheritance of maternal immunity. The problem in this case is more difficult because we cannot tell with certainty whether the immunizing substance passes to the fœtus by the way of the germ plasm, or directly through the fœtal membranes. This difficulty is partially obviated if the immunity is conferred before fertilization of the egg occurs. But here another disturbing factor arises and that is to confer a permanent immunity for extended periods of time. Repeated tests with these alkaloids demonstrated the permancy of the immunity as very marked in this case, so that they were well suited for experiment on this question. He instituted another series of experiments on rabbits, by pairing an immunized mother with a male of normal susceptibility. Here he found a well pronounced immunity conferred upon the progeny for a certain length of time. At the age of three or four weeks, the young were able to stand ten times the dose that was ordinarily fatal, but in a month and a half it had almost entirely disappeared, and in three months the animal yielded readily to the injection of the normal lethal dose. No

[2]Since this was written, Tizzoni and Centanni have published (Cent. für Bakteriologie, Bd. XIII, No. 3.) the results of a similar series of investigations with rabbits on hydrophobia in which they arrive at a contrary conclusion. Their results are however not uniform but they are of interest in this connectiom as showing how important this field is from an experimental standpoint.

permanent immunity was therefore conferred by the mother.

The temporary immunity can be explained on the assumption of the direct transmission of the anti-toxic substance to the young. He continued the test by pairing animals that were descendants from the progeny of immunized ancestors, but in no case were the descendants refractory toward the toxic substance. These results, although not conclusive upon the disputed question because not continued for a sufficient number of generations, are extremely interesting and go to show that the field of bacterial science offers wide and valuable opportunities for lines of investigation upon problems that have a general biological bearing.

Allusion has been made, and this in only the most cursory manner, to some of the more salient lines of work, and it requires no prophetic vision to see that an experimental field which is so suggestive in its infancy as this has proven to be, must in the future yield a rich harvest to patient systematic investigation.